THE BATACEAE IN THE SOUTHEASTERN UNITED STATES[1]

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BATACEAE Martius ex Meissner, Gen. Tab. Diag. 345, 349, Comm. 260. 1842. "Batideae," nom. cons.

(SALTWORT FAMILY)

A unigeneric family distinguished by nearly linear, opposite, succulent leaves, each with a basal appendage and minute stipules; reduced, anemophilous, imperfect flowers, with a nearly closed sac initially enclosing the staminate flower, and with a 4-locular ovary and sessile stigmas in the carpellate flower, a single, basal-parietal, bitegmic, anatropous ovule in each locule; and seeds lacking endosperm. TYPE GENUS: *Batis* P. Br.

1. **Batis** P. Browne, Civil Nat. Hist. Jamaica, 356. 1756.

Strong-scented, sprawling, succulent, nearly glabrous, small shrubs rarely more than 1 m tall, main stems to 2(–4) cm in diameter at the base, major branches arching or prostrate and (*B. maritima*) rooting at the nodes, branchlets erect or drooping, initially quadrangular in transverse section, becoming terete; bark light gray, flaking. Large irregularly shaped crystals (sodium chloride?) in most organs (calcium oxalate crystals also reported), and often apparently with clusters of salt crystals being excreted through fissures in the epidermis. Wood with the vessel elements mostly solitary or in radial multiples, the perforation plates simple, sometimes bearing thin-walled tyloses; xylem parenchyma vasicentric and banded apotracheal with storied cells; rays

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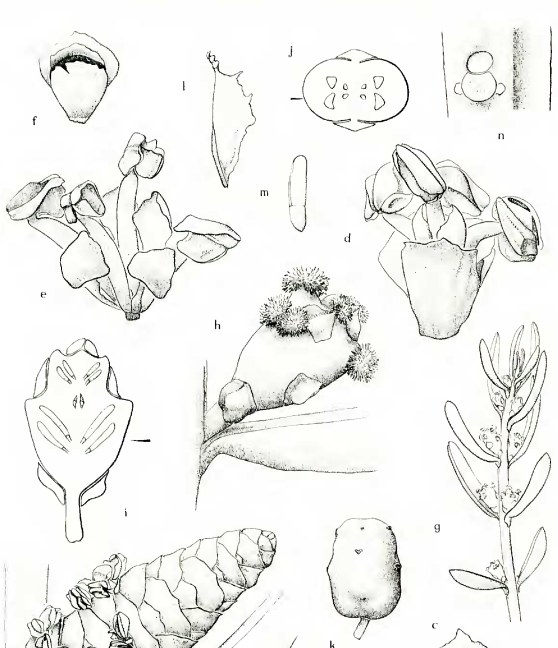

FIGURE 1. **Batis.** a–n, *B. maritima:* a, staminate inflorescence with portion of leaf (note, in region above opened flowers, unopened spathellas alternating in vertical rows with longer bracts), × 5; b, bract from upper part of staminate inflorescence, × 5; c, spathella, abaxial side, before anthesis, × 15; d, same, after anthesis, stamens and tepals of flower protruding, × 15; e, staminate flower removed from spathella, × 15; f, spathella with flower removed to show line of rupture (note thin abaxial surface and thick adaxial surface), × 10; g, branchlet with carpellate inflorescences (note appendage on lower surface of leaf at base), × 1; h, carpellate inflorescence

mostly multiseriate, with crystals (*B. maritima*); ray cells sometimes perforate; fiber-tracheids with minute pits. Leaves simple, sessile, narrowly elliptic to narrowly oblanceolate, in transverse section nearly triangular to nearly terete with the adaxial surface flattened, rounded to acuminate or mucronate at the apex, with a small deltoid appendage below the insertion; stomata paracytic; stipules paired, inserted on the stem, caducous, blunt, minute, succulent, glandular. Plants dioecious [or monoecious]; staminate flowers (*B. maritima*) 4-ranked, in axillary, ellipsoid, turbinate, or subglobose catkins, these sessile or short-pedunculate and sometimes clustered on short branches, each flower subtended by a broadly ovate, obtuse, and often mucronate fleshy bract, margins membranaceous and erose. [Staminate flowers of *B. argillicola* axillary or terminal (when terminal, flanked by a pair of carpellate flowers), not in catkins, sessile or nearly so, usually on short shoots.] Staminate flowers initially enclosed in a sheath (spathella) that dehisces to form a 2- [sometimes 3- or 4-]lipped cup; tepals (staminodes?) 4 (or 5), white, nonvascularized or with an unbranched midvein, unguiculate [or gradually tapered], the limb abaxially cutinized. Stamens longer than the tepals and alternate with them, exserted beyond the subtending bract; filaments glabrous, [winged]; anthers broadly oblong-elliptic, opening by lateral longitudinal slits, dorsifixed, versatile, [connective prolonged]. Pollen grains yellow (dry), subprolate to prolate, 3- or 4-colporoidate (or 3- or 4-loxocolporoidate), the membrane granular, oroid region rounded-lolongate, sexine solid (without columellae), psilate or nearly so, with local thickenings usually near the equator and often near one or both poles. Carpellate flowers [borne singly in the axils of leaves, usually on short shoots or] (in *B. maritima*) 2–14(–24), arranged decussately in short-pedunculate or sessile, axillary, bracteate, fleshy spikelets, these often clustered on short branches; bracts peltate, caducous, usually broadly ovate to orbiculate, sometimes 3-lobed, the margins erose and membranaceous, rounded to acute and often apiculate at the apex, rounded to cordate at the base. Perianth absent. Gynoecium probably 2-carpellate, 4-locular, the locules uniovulate and filled with parenchyma above the ovule; stigmas 2, fimbriate (extruded stigmatoid tissue); ovules bitegmic, crassinucellar, [slightly campylotropous when young], epitropous, erect. Infructescence a green, fleshy, roughly cylindrical(-obconic) syncarp with rounded protuberances corresponding to each carpellate flower (apical flowers often not developing), each seed surrounded by a hard layer (composed of elongate, mostly transverse, pitted cells), these

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(note decussate arrangement of bracts and flowers), × 5; i, diagrammatic vertical section of inflorescence at level marked by arrow on "j," showing ovules, locules filled with parenchyma (stippled), section to one side of attachment of bracts, × 5; j, diagrammatic cross section at level marked by arrow in "i," section passes through ovules in two locules of each of two flowers, × 5; k, mature syncarp (note scars of stigmas and bracts), × 2; l, single endocarp with seed, × 6; m, embryo oriented as in seed and stone, × 6; n, stem with leaf scar and stipules, inflorescence scar above, × 15.

endocarps (pyrenes) narrowly deltoid, strongly compressed, laterally coherent, (locules often sterile). [Or with a septicidally dehiscent, fleshy fruit derived from one flower, with 4 endocarps (pyrenes).] Seeds without (or possibly with a little) endosperm, club shaped, compressed, the testa membranaceous; embryo slightly curved, compressed, filling the seed, the cotyledons fleshy, oblong, plano-convex, the conical radicle pointing toward the hilum. TYPE SPECIES: *B. maritima* L. (*B. californica* Torrey.) (Name probably from Latin, borrowed from Greek, for another maritime plant or, less likely, from Greek *batos*, bramble, because of the superficial similarity of its syncarps to fruits of *Rubus*.)—SALTWORT.

Two species of littoral habitats: *Batis maritima*, common along the east coast of the Americas including the Gulf of Mexico from North Carolina (according to Fulcher not encountered north of South Carolina in recent surveys) to Brazil, throughout the West Indies, along the west coast of the Americas from southern California to northern Peru, on the Galapagos Islands, and in Hawaii (where probably introduced; see Hillebrand, Degener); and *B. argillicola* van Royen, of southern New Guinea and northeastern Australia. There is a doubtful report of an unidentified species of *Batis* in the Marianas Islands ca. 2300 km north of New Guinea (see Fosberg *et al.*).

Only *Batis maritima* is dioecious (*vs.* monoecious), has flowers borne in catkins or spikelets (*vs.* singly or in small clusters), and has highly differentiated bracts subtending the flowers, clawed (*vs.* gradually tapered) tepals, vascular bundles opposite the flat faces of the stem, crystals in parenchymatous tissues, and branches that root. In contrast, some staminate flowers are terminal on short shoots in *B. argillicola*, which also differs in its winged filaments, elongated connectives, smaller leaves, and much stronger tendency toward procumbent cells in the rays. (See further details in van Royen, 1956b, 1958.)

Sunny, periodically wet, saline, maritime habitats seem to be required by both species. They grow in open areas and are often components of mangrove vegetation, especially in association with *Avicennia* (*A. germinans* (L.) L., black mangrove, in the United States). Plants grow either within the stands where abundant light penetrates or adjacent to them, usually on the side opposite open water. In Florida *Batis maritima* has been a major colonizer following loss of mangroves by hurricanes. This species establishes itself on clay, sand, or calcareous substrates on beaches, in salt marshes, in saline mud flats, in hammocks, and in swales on dunes, in addition to growing with mangroves. The plants sometimes form dense tangles and often cover large areas as pure stands. Due to its extensive geographic range and apparent wide ecological amplitude, *B. maritima* is found in association with a variable array of other plants, frequently including *Distichlis spicata* (L.) Greene, and species of *Salicornia* L., *Spartina* Schreber, and *Suaeda* Forskål. ("*Batis* marshes" are characterized by Craighead; see also Chapman, Davis, Harper, and Rzedowski for information concerning habitat and associates.)

Batis maritima tolerates long periods of waterlogging and a wide range of salinity. Penfound and Hathaway reported it to tolerate a range of 1.33–4.97%

salt in soil water, and in reference to the salt water marshes of southern Florida, Davis described plants as growing in the most salty situations that will support plant life.

The spongy syncarps of *Batis maritima* float one to two weeks before decay releases the one-seeded endocarps (pyrenes), which float as long as three months until germination (Guppy, 1906, referred to seeds rather than endocarps). Rooting at the nodes seems to enable the development of clones of this species. In tropical regions it flowers throughout the year; in Florida flowering is between April and late summer, mostly early in the season. Fruits are found from midsummer to late autumn; seedlings have been observed during the same period.

The homology of the petallike appendages that alternate with the stamens is unknown; they have been designated petals, tepals, or (most often) staminodes. Johnson considered the cutinized abaxial surface of the limb and the lack of vascular tissue as evidence against their being staminodes, but in *Batis argillicola* the appendages are usually vascularized. They are sometimes so in *B. maritima* according to Eckardt (1960). The spathella opens to resemble a calyx and has been thus interpreted, but is more likely an involucre. Noting that it bears two crests, that it has two basal appendages (as do the foliage leaves), that its two halves continue the decussate phyllotaxy of the shoot, and that there are leaves morphologically intermediate between it and the foliage leaves, van Royen (1956b) and van Heel argued that the spathella in *B. argillicola* is foliar and is homologous to a pair of opposite bracts. The spathella in *B. maritima* receives a single vascular bundle at the base, and some authors (Dammer, 1892; Johnson; van Tieghem) have regarded it as a single unit. In this species the spathella is usually divided by a transverse apical slit with the edges abutting or one overlapping the other; the adaxial side bears a transverse crest, which matches an abaxial thickening on the bract above and usually protrudes beyond the subtending bract. Dehiscence is through the slit or, according to Johnson, by a transverse rift between the original slit and the crest. A central projection has often been observed in some staminate flowers of *B. maritima*. Although this is suggestive of a rudimentary gynoecium, "imperfect pollen" has been observed in the head of such a structure (Torrey).

It is generally agreed that the gynoecium is composed of two carpels so joined that the lateral bundles, placentae, and septum lie on a median plane (radial to the axis of the spikelet in *Batis maritima*). The ovary is falsely four-locular by a second perpendicular septum. The median carpellary bundles (which are not consistently present) are in the plane of the false septum (see diagrams in Cronquist; Eckardt, 1960; van Heel). The ovary of *B. argillicola* is unilocular at the base. Although the literature is contradictory about the orientation of the raphe of the ovules, my dissections of *B. maritima* showed that it is abaxial, which agrees with the statements of most observers.

Contrary to earlier descriptions, Fulcher encountered scattered ephemeral clusters of unicellular trichomes toward the ends of branches in *Batis maritima*.

The taxonomic placement of *Batis* is a long-standing and unresolved problem. It has no obvious close relatives; thus the many botanists concerned with this aspect of the genus have variously considered allying it with over 25 disparate families or orders, and they have tended to isolate it at high taxonomic levels. It has consistently been taken to comprise a unigeneric family, and it often stands alone as the order Batales (Batidales); Behnke and Turner elevated it even further as the subclass Batidae. The history of the classification of *Batis* and/or lists of families and orders considered as potential relatives are available in several works, including Eckardt (1960), Fulcher, McLaughlin, and Uphof (1930). A summary emphasizing the recent literature follows.

The reduced, imperfect flowers borne in catkins or spikelets (*Batis maritima*) have led some authors to ally *Batis* with the Amentiferae, where it was most recently placed by Benson. With little explanation Hjelmquist has opposed this position. Among the catkin-bearing plants the Salicaceae have received the most attention as potential relatives of *Batis* (see Baillon, van Tieghem), but little evidence supports an affinity with this family. The base chromosome number of the Salicaceae is 19, in contrast with $n = 11$ for *B. maritima*. (Goldblatt and Fulcher independently reported $n = 11$, but Engel & Schmidt reported $n = 9$.) After comparing *Batis* to that family, Fulcher concluded an extensive anatomical-morphological study favoring a relationship with the Urticales, possibly as a derivative of Moraceae. Chiefly on the basis of stem anatomy, McLaughlin favored the Centrospermae over the Salicaceae.

Most authors have treated *Batis* as a member of the Centrospermae (Caryophyllales). In habit *Batis* is similar to succulent, halophytic members of the Chenopodiaceae, a resemblance supported by the reduced, imperfect flowers, scarious, uniseriate (or absent) perianths (as well as staminodes), and compact, bracteate inflorescences found among this family and some of its relatives. Moreover, van Heel pointed out that ovules of *B. argillicola* resemble those of various members of the Centrospermae because only the inner integument forms the micropyle; others (Fulcher, van Tieghem) found the micropyle to be formed of both integuments in *B. maritima*.

Rejection of *Batis* as a member of the Centrospermae reflects the modern trend toward emphasizing a suite of technical characters in circumscribing the group. Characters in conflict with its placement in the Centrospermae include seeds with nearly straight (*vs.* curved or coiled) embryos and no perisperm (Eckardt, 1960, 1976), S-type (*vs.* P-type) sieve-tube plastids (Behnke & Turner; Behnke, 1976a), and binucleate, psilate (*vs.* trinucleate, spinulose, tubuliferous/punctate) pollen grains without columellae (Behnke, 1976b; Fulcher; Prijanto, 1970b; Skvarla & Nowicke). RNA-DNA hybridization (Chang & Mabry) and the chromosome number (Goldblatt) likewise favor exclusion. *Batis* lacks betalain pigments, one of the best-known characteristics of the Centrospermae, but also lacks anthocyanin (Mabry & Turner). Because all of these technical characters—except those connected with the morphology of the pollen and seeds—are reported only for *B. maritima*, confirmatory research on *B. argillicola* is desirable.

Batis maritima also differs from the Centrospermae in that it produces myrosinase. Since this enzyme acts on glucosinolates, its presence supports linking *Batis* to the glucosinolate-producing families of the Capparales (Schraudolf *et al.*). Benzylglucosinolate was later confirmed as present in *B. maritima* (Ettlinger *fide* Mabry, 1976). Essentially the same circle of affinity was indicated when Pulle allied the Batales with the Rhoeadales (brief discussion in Eckardt, 1960, 1964). Other characters that *Batis* shares with members of the Capparales include seeds without endosperm, minute stipules, and paired carpels. Placement in or close to the Capparales is consistent with chromosome data (Goldblatt). Moreover, if *Batis* has parietal placentae, a replum in the ovary, and staminodes, these characters provide additional ties to the Capparales.

The Australian family Gyrostemonaceae also produces glucosinolates (Ettlinger & Kjaer) and, like *Batis*, is outstanding in having these compounds but lacking myrosin cells (Carlquist, Rodman). They are also alike and unusual in their psilate (to slightly scabrous in the Gyrostemonaceae) pollen grains with a solid sexine, although *Batis* differs in having compound apertures without opercula (Erdtman; Prijanto, 1970b). The Gyrostemonaceae resemble *Batis* in the absence of betalain and anthocyanin pigments and in having S-type sieve-tube plastids (Goldblatt *et al.*). Additional similarities include succulence, shrubbiness, wide multiseriate rays, storied xylem parenchyma cells resembling short fibers, linear leaves with minute stipules, and reduced, imperfect flowers with uniovulate locules. Van Royen (1956b) mentioned the "striking resemblance" of *B. argillicola* to *Gyrostemon* Desf., as well as to other groups. The presence of both genera in Australia is consistent with this apparent relationship (Carlquist).

However, Goldblatt *et al.* thought that different chromosome numbers indicate that the relationship between *Batis* and the Gyrostemonaceae might not be close (in Gyrostemonaceae $x = 14, 15$). Other traits by which *Batis* differs from the Gyrostemonaceae are paracytic (*vs.* anomocytic) stomata, opposite leaves, spathellas, fewer stamens, lack of diffuse xylem parenchyma, four-locular ovaries with basal-parietal (*vs.* axile) placentae, seeds without arils and endosperm, and nearly straight embryos (cf. Carlquist, Cronquist, Thorne). Cronquist included the Gyrostemonaceae in the Batales, which he allied to the Capparales. Goldblatt *et al.* favored placement of *Batis* and the Gyrostemonaceae in the Capparales, which is the placement these taxa received from Dahlgren *et al.* It should be noted that pollen of *Batis* and members of the Gyrostemonaceae is anomalous in that order (Erdtman; Goldblatt *et al.*). Furthermore, glucosinolates are not restricted to the Capparales as usually circumscribed; they are reported, for example, in the Caricaceae, Euphorbiaceae, Limnanthaceae, and Salvadoraceae (Rodman).

Carlquist discussed the possible presence of such compounds among the Sapindales. Drawing mostly upon general morphology and wood anatomy, he considered sapindalean affinities for both *Batis* and the Gyrostemonaceae most likely but regarded them as distinct from each other. Some other modern systematists agree that a position in or near this order is best. Takhtajan thought the Bataceae and the Gyrostemonaceae were related and placed both

in the Sapindales. Thorne tentatively put his suborder Batineae "following" the Gyrostemonaceae (in the Sapindineae) among the Rutales.

The salty leaves and stems of *Batis maritima* are sometimes pickled, used as potherbs, and eaten fresh in salads, but the plant is suspected of being poisonous (Duncan; Perkins & Payne). As is true of other halophytes, plants of this species have been burned for ash, which was used in making soap, glass, and medicines. In countries where Spanish is spoken, the colloquial name *barilla* is (was?) commonly associated with the ash and plants of *B. maritima* but is not unique to this species. Variously derived preparations have evidently been used to prevent and treat skin disorders, tuberculosis, syphilis, scurvy, and ulcers, and some have been used as a diuretic, as an analeptic, and to remove stones from the bladder and kidneys (see Burlage, Descourtilz, Grosourdy). In Hawaii *B. maritima* has been planted on reclaimed land to suppress wind-blown dust.

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